Production Study of the Population of the Pine Caterpillar (Dendrolimus spectabilis Butler)

Production Study of the Population of the Pine Caterpillar (*Dendrolimus spectabilis* Butler)

Kihachiro KIKUZAWA* and Tooshu FURUNO**

マツカレハ幼虫個体群の生物生産の研究

菊沢喜八郎*・古野東洲**

CONTENTS

RÉSUMÉ

Productivity of a pine caterpillar population was investigated in the present study. The changes in larval density of the pine caterpillar population were estimated by the fecal-pellets counting method and by the direct counting method at a pine stand in a nursery. The food consumption, assimilation, respiration and growth were also measured in the laboratory. The total food consumption, assimilation, respiration and growth of the population were calculated utilizing the individual values and population density.

An individual larva consumed about 14.0 g of pine needles over one growing season. From which 11.2 g was defecated as feces, and the rest 2.8 g was assimilated. 2.3 g, or eighty per cent of the assimilated matter was used for respiration and 0.5 g was used for growth of larval body weight.

Larval density was estimated at about 63 individuals per square meter in September 1967, which decreased to about 6 individuals per square meter in July 1968 (at the time of pupation).

The total food consumption of the larval population over one growing season was estimated at 133 g/m^2/year. From this 133 g, 106 g fell as feces and 27 g were assimilated

* Department of Forestry, Faculty of Agriculture, Kyoto University, Kyoto, Japan
** School Forest of Kyoto University, Kyoto, Japan

by the population. 21 g, or eighty per cent of the assimilated matter was used as respiration and 6 g was used for population growth.

Positive correlation was observed between population growth and biomass of larval population. Food consumption of a population also positively correlated with the biomass.

要　　旨

マツカレハ幼虫個体群の生産を，苗圃の実験個体群について調べた。幼虫の密度推定は糞数法および直接観察によって行なった。幼虫1個体当りの食物消費量，同化量，呼吸量，生長量は実験室において飼育個体を用いて測定した。個体群の食物消費量，同化量，呼吸量，生長量は飼育個体の各量と個体数変動とから測定した。

一頭の幼虫は一生育期間に平均約 14.0 g（乾重）のクロマツの葉を消費した。そのうち 11.2 g は排出され，2.8 g が同化された。同化量は80%すなわち 2.3 g が呼吸として消費され，生長量は 0.5 g であった。

幼虫の密度は，実験開始時の1967年9月には63頭/m^2 であったが，蛹化時の1968年7月には6頭/m^2 にまで減少した。

個体群としては一生育期間に 133 g/m^2 のクロマツの葉を摂食した。そのうち 106 g は糞として林床に落下し，27 g が個体群によって同化された。同化量のうち 21 g は呼吸として消費され，個体群の生長量は 6 g であった。

個体群の生長量と個体群の現存量との間には正の相関が認められた。個体群の積算摂食量と個体群現存量との間にも正の相関が認められた。

INTRODUCTION

Productivity of animal populations has been investigated in various kinds of habitats (CLARKE 1946[1]; ENGELMANN 1966[2]; REICHLE 1967[3]; RICKER 1946[4]; SMALLEY 1960[5]). However, few production studies have been made concerning the population of forest defoliators, since almost all attention has been paid to the life histories of the insect pests and their population dynamics (KLOMP 1966[6]; MORRIS 1955[7]). Although undoubtedly population dynamics is the main concern in forest entomology, population dynamics alone may be insufficient for the complete understanding of the dynamics of the forest ecosystem. Since the amounts of food consumed by a population of defoliators change with their ages even in a generation, thus this knowledge is necessary in the production study of the forest ecosystem as well as in the population bio-economics itself.

From this view point, several authors have attempted to investigate the amounts of food consumed by an individual larva, for example, the food consumption of the pine looper (*Buparus piniarius*) was measured by SCHWERDTFEGER (1930[8]), and that of the pine caterpillar by FURUNO (1963[9]). Few studies, however, on food consumption of a population have been appeared.

In a previous paper, the authors estimated the amounts of pine needles consumed by natural populations of pine caterpillars (KIKUZAWA and FURUNO 1968[10]), but they did not clarify the changes of food consumption in relation to changes of population density and individual weight. In the present study, the changes in larval density of the pine caterpillar population were estimated. The food consumption of individual larva was also measured in the laboratory. The total food consumption of a population is estimated by the above two components.

MATERIAL AND METHOD

The pine caterpillar, chosen for this investigation, generally has one life cycle a year near Kyoto. The adult moths emerge in late July and in early August lay masses of eggs on pine needles which take about two weeks for incubation. First instar larvae begin to consume needles in late August. They grow until early November when they hibernate. In April of the following year, the fourth instar larvae begin to consume needles again. In early July, fully grown larvae (7th instar) pupate in cocoons. It takes about two weeks for emergence.

Thirteen hundred larvae collected from pine trees in Kyoto city were released on 7 September 1967 in a pine stand at a nursery comprises of 37 pine trees (*Pinus thunbergii*).

Six representative trees were chosen and the larval numbers on each tree were counted at about one-month intervals except in winter. Ten fecal-pellet collectors, each 25 cm × 25 cm in surface area, were set on the stand floor, and the fecal pellets fallen into the collectors were counted, oven dried and weighed. The leaf litter and the leaves cut uneaten by the lavae fallen into the collectors were also collected, oven dried and weighed.

Individual larvae were reared in the laboratory to estimate the amounts of food consumption, the number and the weight of fecal pellets, and the amount of respiration and growth. The difference in the length of the pine needles fed at the beginning and that which remained uneaten at the end of experiment was converted into dry weight which is an estimate of the amount of food consumed by larva during that period. Sixteen individuals were reared.

One larva and small petri dish containing 5 cc of KOH soluiton were kept in an air tight glass container, 9 cm in diameter and 5 cm in depth, for 24 hours to measure respiration. The carbon dioxide absorbed by the KOH solution after 24 hours was estimated by titration with 0.2 N HCl. Respiration measurements were conducted under room temperature condition which varies from 23°C to 30°C. The respiratory rates measured were recalculated to provide values at 30°C assuming that Q_{10} value is 2.0.

Frequent measurements of body weights provided values for the growth of the larvae.

Calorific values of larval body, fecal pellet and pine needles were measured utilizing the bomb calorie meter.

RESULTS

I. Metabolism Of Individual Larva

1. Food Consumption

In the present study where the larvae were fed needles of *Pinus thunbergii*, the amounts of pine needles consumed by an individual larva during one growing season averaged 14.0 g in oven-dry weight, while FURUNO (1963)[9] obtained about 11.1 g when fed with needles of *P. densiflora*. Although average obtained in the present study was somewhat larger than that of FURUNO, this difference can not be considered significant, since there were considerable variations among individuals.

The amounts of food consumption from the beginning of the experiment (time t_0) to time t, or the cummulative amounts of food consumption ($\bar{C}$), were plotted semi-logarithmically against time t as shown in Figure 1, where the ordinate is logarithm of C, and the abscissa is time t. Roughly speaking, the cummulative food consumption ($\bar{C}$) is expected to increase exponentially with time t, except during the periods of hibernation and before casting off and before pupation.

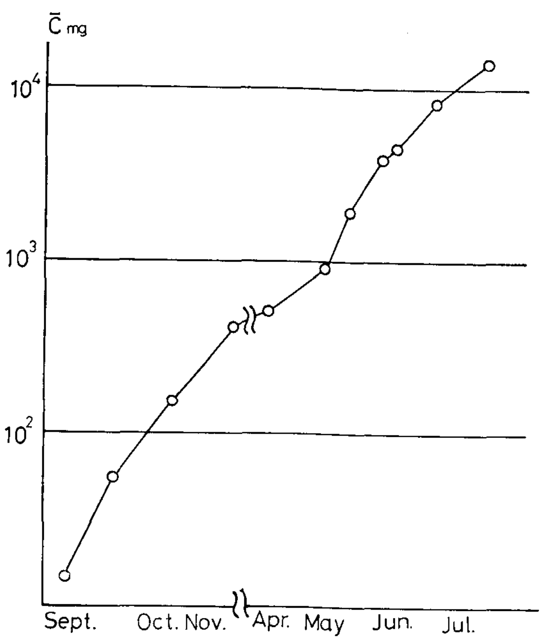

Fig. 1. The cummulative amounts of food consumption ($\bar{C}$) by and individual larva.

2. Feces

Relationship between food consumption and defecation can be expressed by the following formula :

$$\Delta\bar{C} = \Delta\bar{A} + \Delta\bar{F} \quad \cdots\cdots\cdots(1)$$

where, $\Delta\bar{C}$, amount of food consumption during a time unit

$\Delta\bar{A}$, amount of assimilation during a time unit

$\Delta\bar{F}$, amount of feces during a time unit

The relationship between the amount of food consumed and the amount of feces defecated during a certain unit of time (20 days) is shown in Figure 2 on a double logarithmic scale. The decline of the regression line in the figure is unity as has already shown by FURUNO (1963)[9] : food consumption and defecation is proportional or the assimilation ratio is constant. The regression equation is

$$\Delta\bar{C} = 1.25\,\Delta\bar{F} \quad \cdots\cdots\cdots(2)$$

From equation 1 and 2, the following can be obtained.

$$\Delta\bar{A} = 0.2\,\Delta\bar{C} \quad \cdots\cdots\cdots(3)$$

In the present experiment, the mean number of fecal pellets was 22.6 per day per

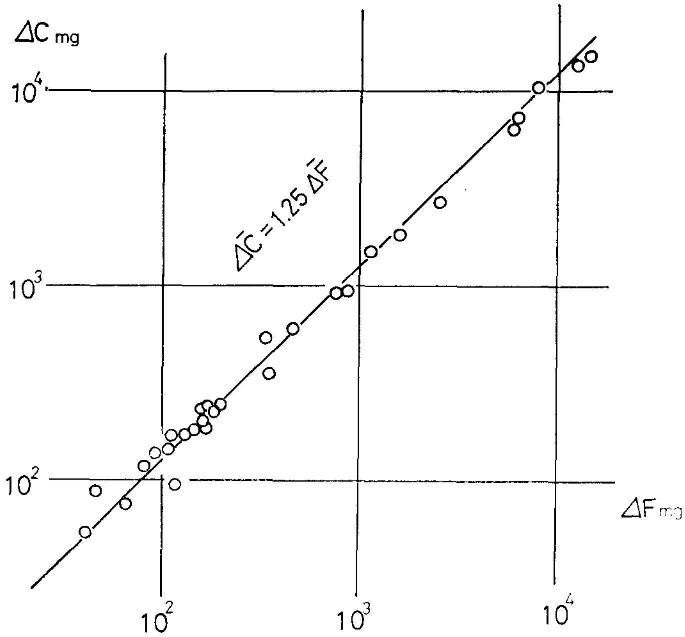

Fig. 2. Relationship between food consumption ($\Delta\bar{C}$) and defecation ($\Delta\bar{F}$) during a certain unit of time (20 days).

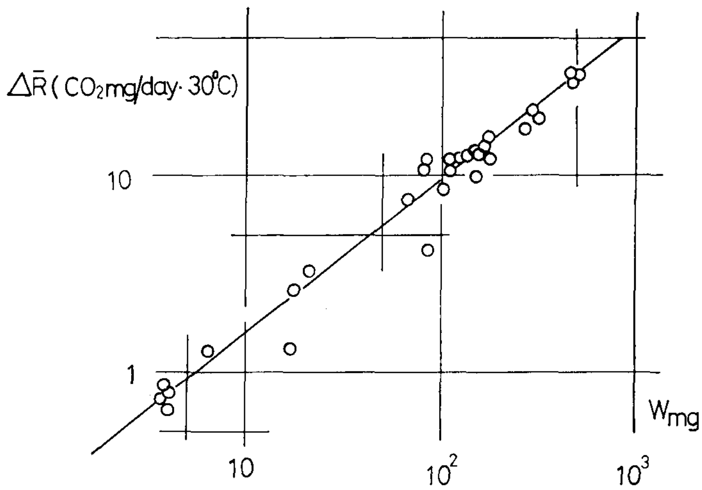

Fig. 3. Relationship between respiratory rate per individual larva per day at 30°C ($\Delta\bar{R}$) and larval body weight (W).

individual which was somewhat larger than 13—19 per individual per day obtained by FURUNO (1963)[9]. The reason for this difference could not be clarified.

3. Respiration

The respiratory rates per day per individual larva are plotted against body weight as shown in Figure 3 on a double logarithmic scale. The regression line in the figure could be expressed as

$$\Delta\bar{R}=0.26\ W^{0.77} \quad \cdots\cdots\cdots\cdots(4)$$

where $\Delta\bar{R}$ is the respiratory rates expressed as CO_2 mg per day per individual and W is the body weight.

The assimilated matter is used as respiration and the residue is used for growth. This relation is expressed as

$$\Delta\bar{A}-\Delta\bar{R}=\Delta W \quad \cdots\cdots\cdots\cdots\cdots(5)$$

where ΔW is the increase in body weight during the time unit concerned. From equation 1 and 4

$$\Delta\bar{R}=\Delta\bar{C}-\Delta\bar{F}-\Delta W \quad \cdots\cdots\cdots(6)$$

If $\Delta\bar{C}$, $\Delta\bar{F}$ and ΔW were measured, $\Delta\bar{R}$ could be estimated utilizing equation 6.

As the respiratory rates obtained utilizing the respiration chamber are considered to be the rest metabolic rate (RMR) (SAITO 1968) which is lower than that in the field, equation 6 was used for the calculation of population value.

4. Growth

The growth curve of a representative individual is shown in Fig. 4. Body weight increased from the beginning of the experiment until early November when the larvae began to hibernate. From the following April it increased again rapidly with time. The growth curve of the pine caterpillar in its active periods can be considered to be approximately exponential. The amount of growth over one growing season is about 500 mg or 2791 cal.

Food consumption, defecation, assimilation, respiration and growth of an individual larva over one growing season are shown in Table 1. A pine caterpillar consumes about 14.0 g or 703600 cal of pine needles from which 11.2 g (54700 cal) is defecated as feces and 2.8 g (15660 cal) is assimilated. Eighty per cent of the assimilated matter is used for respiration. Only four per cent of the consumed matter is used for growth of larval body weight.

II. Estimation Of Population Density

Population densities were estimated by both direct counting and the fecal-pellets method. The advantages of the latter method when applied to natural populations of pine caterpillars was discussed in a previous paper.

The larval densities per square meter thus obtained are shown in Figure 5 as a survivourship curve.

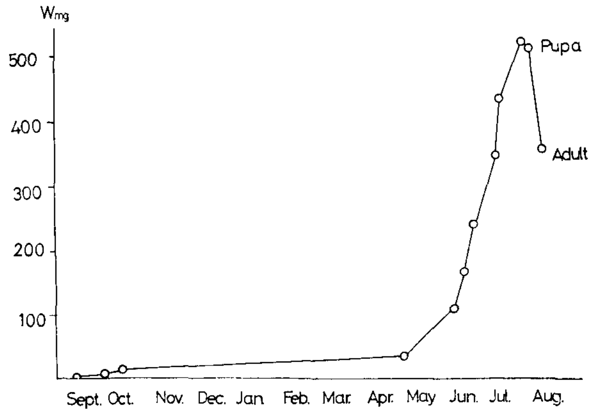

Fig. 4. Growth curve of a representative individual.

Table 1. Food Consumption, Defecation, Assimilation, Respiration, and Growth of an Individual Larva over One Growing Season.

Consumption	$\bar{C}$	14.0 g		
Defecation	$\bar{F}$	11.2	$\bar{F}/\bar{C}$	0.80
Assimilation	$\bar{A}$	2.8	$\bar{A}/\bar{C}$	0.20
Respiration	$\bar{R}$	2.3	$\bar{R}/\bar{C}$	0.16
Growth	$\bar{G}$	0.5	$\bar{G}/\bar{C}$	0.04

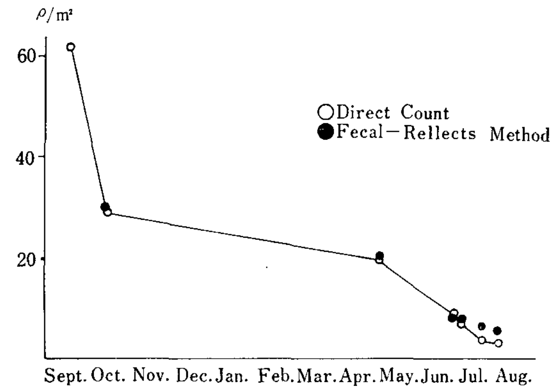

Fig. 5. Suvivorship curve of the larval population.
○ : estimated larval numbers per square meter by the direct counting method
● : estimates by the fecal-pellets counting method

Although individual numbers decreased rapidly from September to November, mortalities during the periods of hibernation and the succeeding larval stage were not so high. This tendancy of the survivour curve is simillar to that obtained formerly by KANAMITSU.[12]

III. Production Of Population

In this study, the production of entire population, i. e., both the production of the survivors and the production of dead individuals up to their time of death, has been undertaken.

Now let the amount of food consumed by the population be ΔC, defecation be ΔF, respiration be ΔR and growth be ΔG during a unit of time from t_1 to t_2. Similar to the case of an individual, the next relation would be expected.

$$\Delta C = \Delta F + \Delta R + \Delta G \qquad \cdots\cdots(7)$$

On the other hand, let biomass at time t_1 be B_1 and t_2 be B_2, respectively, and the mortality during this time unit be ΔD. The following relation would be obtained (KIRA et al 1967).[13]

$$\Delta C + B_1 = \Delta F + \Delta R + \Delta D + B_2 \qquad \cdots\cdots(8)$$

From equation 7 and 8

$$\Delta B = B_1 - B_2 = \Delta G - \Delta D \qquad \cdots\cdots(9)$$

From equation 9, it is apparent that the increment of biomass is not true growth but difference in the amount of growth and death. Now let population density at time t_1 and t_2 be ρ_1 and $(\rho_1 - \Delta\rho)$, and individual weight at t_1 and t_2 be W_1 and $(W_1 + \Delta W)$. Hence B_1 and B_2 would be expressed as

$$B_1 = W_1 \rho_1 \qquad \cdots\cdots(10)$$

$$B_2 = (W_1 + \Delta W)(\rho_1 - \Delta\rho) \qquad \cdots\cdots(11)$$

and

$$\Delta D = W_1 \Delta\rho + \sum_{1}^{\Delta\rho} \Delta W_d \qquad \cdots\cdots(12)$$

where ΔW_d is the amount of growth of dead individuals from time t_t to the time of death.

Substituting equations 10, 11 and 12 into 9,

$$\Delta C = \Delta F + \Delta R + (\rho - \Delta\rho)\Delta W + \sum \Delta W_d \cdots\cdots(13)$$

from equations 7 and 13

$$\Delta G = (\rho_t - \Delta\rho)\Delta W + \sum \Delta W_d \qquad \cdots\cdots(14)$$

Thus, the growth of population is the sum of the growth of the survivors from t_1 to t_2 ($\Delta G_s = (\rho_1 - \Delta\rho)\Delta W$) and the growth of individuals which die during t_1 and t_2 ($\Delta G_d = \sum \Delta W_d$). Similar considerations must be applied for ΔC, ΔF and ΔR; for example, food consumption of survivors (C_s) and that of dead individuals (C_d).

$$\Delta C = \Delta C_s + \Delta C_d \qquad \cdots\cdots(15)$$

$$\Delta F = \Delta F_s + \Delta F_d \qquad \cdots\cdots(16)$$

$$\Delta R = \Delta R_s + \Delta R_d \qquad \cdots\cdots(17)$$

1. Food Consumption of a Population

Equation 15 would be easily understood by referring to Figure 6 where the abscissa is the cummulative amount of food consumed by an individual ($\bar{C}$) and the ordinate is the population density (ρ). The curve in Figure 6 is expressed as

$$\rho = f(\bar{C}) \qquad \cdots\cdots\cdots\cdots\cdots\cdots(18)$$

This relation is considered to be obtained from the following two relations by diminishing time t (NEESS and DOUGDALE[14]).

$$\rho = g(t) \qquad \cdots\cdots\cdots\cdots\cdots\cdots(19)$$

$$\bar{C} = h(t) \qquad \cdots\cdots\cdots\cdots\cdots\cdots(20)$$

where all the variables such as ρ, $\bar{C}$, etc., are treated as continuous ones. The food consumption of the population, C, is considered the area under the curve (area, ACDE) and expressed as,

$$C = \int_{\rho_0}^{\rho_t} \bar{C}\, d\rho$$

In Figure 6, area ABE and BCDE correspond to C_s and C_d in equation 15, respectively.

The food consumption of the pine caterpillar population is shown in Figure 7. The amount consumed by the population over one growing season was 133 g/m² (668500 cal/m²); from the beginning of the experiment to hibernation was 11 g (55300 cal) and after hibernation was 12g (613200cal). The latter was conspicuously larger than the former. C_s and C_d were 83 g/m² and 50 g/m², respectively.

2. Growth of Population

Similar to the case of food consumption, population growth is obtained letting density ρ be the function of weight W by diminishing time t from the survivor and growth curve as,

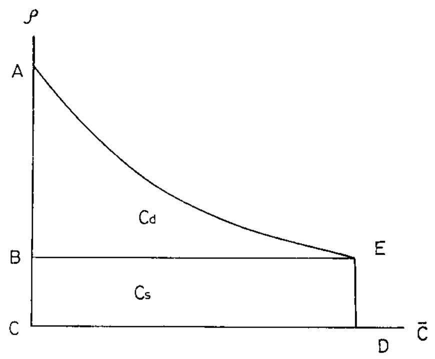

Fig. 6. Schematic figure represents the food consumption of a population, C_s is food consumption of survivors and C_d is that of dead individuals.

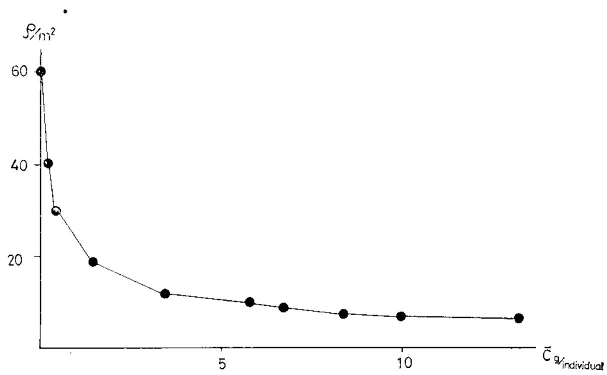

Fig. 7. Food consumption of the pine caterpillar population.

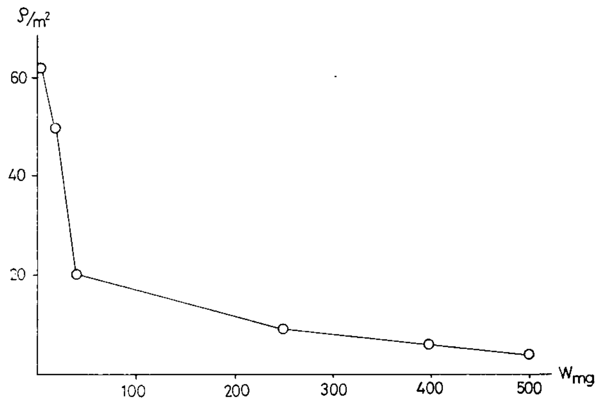

Fig. 8. Growth of the pine caterpillar population.

$$\rho = k(W) \qquad \cdots\cdots (22)$$

and, G, population growth, would be obtained as an integration of equation 22 as,

$$G = \int_{W_0}^{W_t} \rho \, dW \qquad \cdots\cdots (23)$$

This relation is shown in Figure 8. The population growth of pine caterpillar over one growing season was about 6 g (33500 cal)/m². Both the growth of the survivor and that of the dead individuals were 3 g/m².

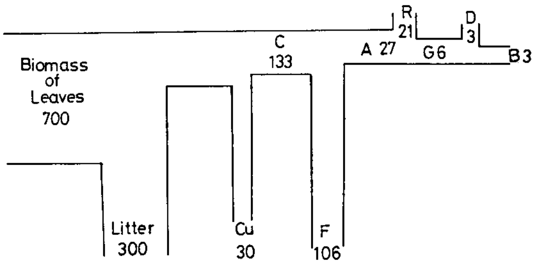

Fig. 9. Flow diagram of dry matter in the pine stand. All the figures are represented as dry matter (gram) per square meter per year.
Cu : Pine needles cut uneaten by the larval population
C : Pine needles consumed by the larval population
F : Feces defecated by the larval population
A : Assimilation
R : Respiration
G : Growth of the population
D : Death, or the growth of the dead individuals
B : Biomass of the pupae

3. Contribution of the Pine Caterpillar Population as a Component of the Forest Stand

The amount of defecation, assimilation and respiration were calculated by utilizing equations 2 and 7. All the amounts mentioned above were shown in Figure 9 as a flow diagram of dry matter in the pine stand per year per square meter.

From about 700 g of leaves on the canopy 300 g fell as leaf litter and 163 g was used by the caterpillar population, from which 30 g fell uneaten and 133 g was consumed by the population. From this 133 g, 106 g fell as feces and 27 g was assimilated.

About eighty per cent or 21 g of the assimilated matter was used as respiration and twenty per cent or 6 g were used for population growth.

The biomass at the time of pupation was 3 g which amounted to only 2.3 per cent of the consumed matter.

DISCUSSION

There are several problems in the methods used in the present study. In the laboratory experiments, there are considerable variations in the metabolic rates among individuals, thus more precise measurements using larger numbers of individuals would be required. The estimation methods of density are rather precise as mentioned before and these methods could be applicable for field study in the future.

The effects of the consumption of population on the total forest ecosystem must be considered here. Considering an individual tree there were several experiments of artificial defoliation, among which FURUNO (1964)[15] investigated the effects of defoliation on tree growth. Considering insects, there was the concept of KZ or the individual numbers which would cause considerable damage to the forest (TACHIBANA and NISHIGUCHI 1968)[16]. However, this concept can not predict damage since individual numbers change with time and also the amounts of food consumed by a population is not only related to individual numbers but also to body weight. Consequently, it would be better to use biomass rather than individual number as a variable related to the food consumption of a population.

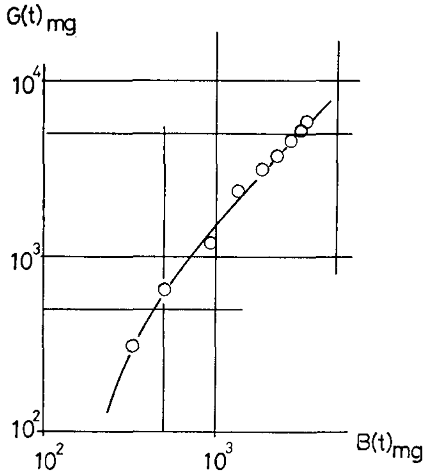

Fig. 10. Relationship between growth and biomass

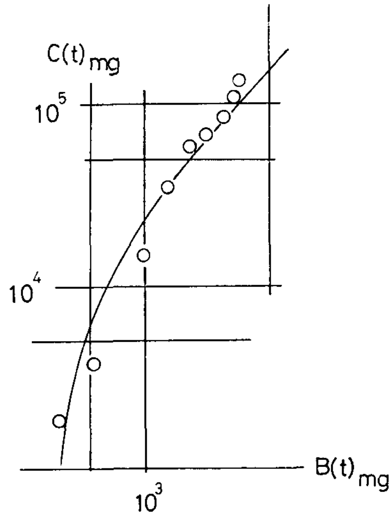

Fig. 11. Relationship beetween food consumption and biomass of the larval population.

In Figures 10 and 11, the growth from the beginning of the experiment, time t_0, to time t, G(t), and food consumption from time t_0 to t, C(t), are plotted against biomass at time t, B(t), on a double logarithmic scale. In these two figures, positive correlations were observed between C(t), G(t) and B(t).

These relations were analyzed by using the NEESS and DOUGDALES formulae (1959) : ρ and W are both assumed to be exponential functions of time t as

$$\rho=\rho_0 \exp(-\lambda t) \quad \cdots\cdots(24)$$

$$W=W_0 \exp(\delta t) \quad \cdots\cdots(25)$$

Biomass, B, is expressed as

$$B=\rho_0 W_0 \exp\{(\delta-\lambda)t\} \quad \cdots\cdots(26)$$

Diminishing time t from equation 24 and 25

$$\rho=\rho_0 W_0^{\lambda/\delta} W^{-\lambda/\delta} \quad \cdots\cdots(27)$$

From equations 23 and 27

$$G=\int_{W_0}^{W_t} \rho\, dW=\int_{W_0}^{W_t} \rho_0 W_0^{\lambda/\delta} W^{-\lambda/\delta} dW$$

$$=\rho_0 W_0^{\lambda/\delta} \frac{W^{-\lambda/\delta}}{1-\delta}-\frac{\rho_0 W_0}{1-\lambda/\delta} \quad \cdots\cdots(28)$$

Substituting 25 and 26 into 28, the following would be obtained

$$G=\frac{\delta}{\delta-\lambda}(B-B_0) \quad \cdots\cdots(29)$$

Thus, growth amounts are proportional to biomass, if δ and λ are constant, Equation 29 is shown in Figure 10 as a C–D curve (SHINOZAKI and KIRA; 1961[17]). The expected curve fits to the observed values fairly well. Assuming that growth ratio, g, is constant over one growing season, the following equation would be expected similar to the case of growth.

$$C=\frac{\delta}{g(\delta-\lambda)}(B-B_0) \qquad \cdots\cdots(30)$$

As shown in Figure 11, equation 30 and the observed values are not too well matched. This may be due to assuming growth ratio, g, to be constant. Further experiment and analysis would be required.

LITERATURE

1) CLARKE, G. L. : Dynamics of production in a marine area. Ecol. Monogr. 16 : 321—337, 1946
2) ENGELMANN, M. D. : Energetics, terrestrial field studies and animal productivity. *Advances in Ecological Research* vol. 3 : 73—115, 1966
3) REICHLE, D. E. : Radioisotope turnover and energy flow in terrestrial isopod. Ecol. 48 : 351—376, 1967
4) RICKER, W. E. : Production and utilization of fish populations. Ecol. Monogr. 16 : 373—391, 1946
5) SMALLEY, A. E. : Energy flow of a salt marsh grasshopper population. Ecol. 41 : 672—677, 1960
6) KLOMP, H. : The dynamcs of a field population of the pine looper, *Buparus piniaris* L. (Lep., Geom.). *Advances in Ecological Reasearch* vol. 3 : 207—305
7) MORRIS, R. F. : The development of sampling techniques for forest insect defoliators, with particular refernce to the spruce budworm. Canad. J. Zool. 33 : 225—294, 1955
8) SCWERDTFEGER, F. : Untersuchungen über Dauer das Eistadiums, Wachstum und Stoffwechsel des Kiefernspanners (*Buparus piniarius* L.) Z. ang. Ent. 16 : 513—526, 1930
9) FURUNO, T. : On the feeding quantity of the pine caterpillar (*Dendrolimus spectabilis Butler*). J. Jap. For. Soc. 46 : 52—59, 1964 (In Japanese with English summary)
10) KIKUZAWA, K. and T. FURUNO : The estimation of population density of the pine caterpillar, *Dendrolimus spectabilis* BUTLER. Bull. Kyoto Univ. For. 40 : 7—15, 1968
11) SAITO, S. : Productivity of high and low density populations of *Japonaria laminata armigera* (Diplopoda) in a warm-temperate forest ecosystem. Res. Popul. Ecol. 9 : 153—166, 1968
12) KANAMITSU, K. : Survival curves of the population of *Dendrolimus spectabilis* BUTLER (Lep., Lasiocampidae). Res. Popul. Ecol. 4 : 60—64, 1962
13) KIRA, T. et al. : Comparative ecological studies on three main types of forst in Thailand 4. Dry matter production with special refernce to the Khao Chong rain forest. Nature & Life in SE Asia : 5 : 149—174
14) NEESS, J. and DOUGDALE, R. : Computation of production for populations of aquatic midge larvae. Ecol. 47 : 425—430, 1959
15) FURUNO, T. The effects of the feeding-damage of the pine-caterpillar (*D. spectabilis* BUTLER) upon the red-pine (*P. densiflora* S. Z.) by artificial defoliation. J. Jap. For. Soc. 46 : 52—59, 1964 (In Japanese with English rummary)
16) TACHIBANA, K. and C. NISHIGUCHI : *Waldhygiene*, 233 pp. Tokyo, 1968 (In Japanese)
17) SHINOZAKI, K. and T. KIRA : The C—D rule, its theory and practical uses (intraspecific competition among higher plants X) J. Biol. Osaka City Univ. 12 : 69—82, 1961